

Adaptive strategies and environmental significance of lingulid brachiopods across the late Permian extinction



Renato Posenato^{a,*}, Lars E. Holmer^b, Herwig Prinoth^c

^a Dipartimento di Fisica e Scienze della Terra, Università di Ferrara, Polo scientifico-tecnologico, Via Saragat 1, 44121 Ferrara, Italy

^b Department of Earth Sciences, Palaeobiology, Uppsala University, SE-752 36 Uppsala, Sweden

^c Museum Ladin Ciastel de Tor, 39030 San Martino in Badia, Bolzano, Italy

ARTICLE INFO

Article history:

Received 28 October 2013

Received in revised form 20 January 2014

Accepted 31 January 2014

Available online 10 February 2014

Keywords:

Late Permian extinction

Early Triassic recovery

Brachiopoda

Evolutionary paleoecology

Southern Alps

ABSTRACT

Linguliform brachiopods are traditionally considered a conservative group which seems to pass through the late Permian extinction without any significant loss and even appear to thrive immediately after the extinction peak. In the Southern Alps, lingulids are very common in the post-extinction Mazzin Member (early Induan) of the Werfen Formation. Sparse occurrences are also known in the overlying Siusi and Gastropod Oolite members (late Induan and early Olenekian in age respectively). The recent discovery of well preserved specimens from a pre-extinction bed of the Bellerophon Formation (Changhsingian) has permitted a detailed comparative analysis, mostly based on the interior characters, preserved in the lingulid succession from across the extinction beds. The following effects on the lingulid populations have been analyzed: i) change in taxonomic assessment; ii) adaptive strategies during the surviving and recovery phases; and iii) environmental proxy connected with the killing mechanisms of the late Permian extinction.

The pre-extinction individuals belong to *Lingularia? cf. smirnovae* Biernat and Emig, a species that is characterized by large-sized shells with a short lophophoral cavity. The post-extinction populations belong to different species and, probably, even to a different genus. The first post-extinction population (early Induan), with small-sized shells and long lophophoral cavity, has been referred to *Lingularia yini* (Peng and Shi). It records the most severe effects of the late Permian extinction on the marine ecosystems. The late Induan–Olenekian *Lingularia borealis* (Bittner), with large sized shells and long lophophoral cavity, appears during the first phase of the Triassic biotic recovery.

The main adaptive strategies of *Lingularia yini*, in comparison with the Permian species, include: i) shell miniaturization; ii) increasing of the lophophoral cavity surface (respiratory surface); and iii) increasing of shell width/length ratio. These modifications are interpreted as adaptations towards warming and hypoxia, two main killing mechanisms of the marine biota. The recovery species *Lingularia borealis* maintains a large lophophoral cavity, indicating an adaptation towards predominant low oxygenated bottom marine waters.

The appearance and the great abundance of *Lingularia yini* in the Mazzin Member (early Induan) represent a proxy of dysaerobic conditions, which determined the appearance of the second phase of the Lilliput biota, characterized by the definitive disappearance of the rhynchonelliform brachiopods and calcareous algae in the Southern Alps.

© 2014 Elsevier B.V. All rights reserved.

1. Introduction

The late Permian extinction (LPE) was the most severe biotic crisis of the Phanerozoic, with an extinction rate of about 90% of marine species (e.g., Raup, 1979; Erwin, 2006; Knoll et al., 2007). Many authors consider the extinction of marine animals as taxonomically and physiologically selective. The marine animals with a low basal metabolic rate and heavy calcium carbonate skeletons suffered the loss of 81% of the genera, while those with a high basal metabolic rate, more

efficient circulatory and respiratory systems, and with calcium carbonate skeleton but physiologically able to buffer the pH of body fluids or without carbonate skeletons suffered only 38% of extinction at generic level (e.g., Knoll et al., 1996, 2007; Bambach et al., 2002; Pörtner et al., 2005; Payne and Clapham, 2012; Clapham et al., 2013).

Rhynchonelliformea, the most diversified upper Paleozoic brachiopod group, characterized by articulated calcitic shells and low basal metabolic rate, suffered a very high extinction rate, reaching 86.1% on the generic level. In contrast, Linguliformea, represented in the late Paleozoic by the order Lingulida (or lingulids herein), are characterized by inarticulate organophosphatic stratiform shells. The lingulids seem to pass through this extinction without losses, becoming very abundant in the beds located just above the extinction peak, when the marine

* Corresponding author. Tel.: +39 532 974736; fax: +39 532 974767.

E-mail addresses: renato.posenato@unife.it (R. Posenato), lars.holmer@pal.uu.se (L.E. Holmer), herwig@museumladin.it (H. Prinoth).

ecosystems show the most stressed and hostile environmental conditions (e.g., Broglio Loriga et al., 1980; Xu and Grant, 1994; Rodland and Bottjer, 2001; Peng et al., 2007). Therefore, the lingulids have been considered as “disaster species” (Rodland and Bottjer, 2001). The great abundance and cosmopolitan distribution of the lingulids during the earliest Triassic are related to their wide tolerance towards fluctuations of oxygen, temperature, and acidity (e.g., Wignall, 2001; Heydari and Hassanzadeh, 2003; Farabegoli et al., 2007; Payne et al., 2007; Svensen et al., 2009; Wignall et al., 2009; Brand et al., 2012; Payne and Clapham, 2012).

The extant lingulids differ from the extant rhynchonelliforms mainly in life habit (infaunal vs. epifaunal behavior), larval trophism (planktotrophic vs. lecithotrophic), shell mineralogy (organophosphatic vs. calcitic) and a greater tolerance towards strong salinity fluctuations and poorly oxygenated waters. Lingulids are preadapted towards hypoxia, probably because of their infaunal life habit. This adaptation has been related to the hemerythrin, a respiratory pigment contained within the coelomocytes of the coelomic fluid (e.g., Manwell, 1960; Robertson, 1989; Emig, 1997).

In the Southern Alps, the lingulids have a stratigraphic distribution which spans the LPE. This distribution, with remarkable fluctuations of individual abundance, has permitted us the analysis of the variations of taxonomy and shell morphology in order to recognize the surviving strategies carried out during the post-extinction phase. The older population, representative of the pre-extinction phase and coming from the upper Permian beds of the Bellerophon Formation (Prinoth, 2013), has been compared to three younger populations located in the lower Werfen Formation (Early Triassic), which records the effects of extinction on the marine ecosystems (e.g., Broglio Loriga, 1968; Broglio Loriga et al., 1980, 1988; Wignall and Hallam, 1992; Twitchett and Wignall, 1996; Farabegoli et al., 2007; Groves et al., 2007; Posenato, 2009; Brand et al., 2012). Other sparse specimens originating from the Lower Triassic succession of central Hungary have been also considered (Broglio Loriga et al., 1990). In order to investigate morphological (outer and inner shell morphology) and physiological (e.g., the respiratory efficiency) adaptations related to environmental changes (e.g., dysoxia and acidification), specimens with clearly detectable internal characters have been used. The morphological and physiological adaptation related to the individual size, stratigraphic distribution and abundance of

the lowermost Triassic lingulids provides new insights on the occurrence and sequencing of dysoxia and warming in the western Tethys.

2. Stratigraphic setting

2.1. The upper Permian lingulids

The Bellerophon Formation is an overall transgressive sedimentary succession composed of sulfate evaporites, dolomites and skeletal limestone of marginal to fully marine environments. This succession records the very last moment of the Paleozoic life of shallow marine environment before the LPE (e.g., Broglio Loriga et al., 1988; Posenato, 2010; Brand et al., 2012). Despite the long lasting stratigraphic and paleontologic research (e.g., Stache, 1877, 1878; Merla, 1930; Broglio Loriga et al., 1988; Posenato, 1998; Posenato and Prinoth, 1999; Posenato, 2001, 2010), upper Permian lingulids in the Southern Alps are very rare. The material here analyzed has been recently discovered at Monte Balest, near Ortisei (Prinoth, 2013; Fig. 1).

The lingulids from the Monte Balest are contained within the transgressive system tract of the 4th sedimentary sequence (sensu Massari and Neri, 1997; Posenato, 2010) which is mostly composed of sandstone, marlstone, marly and sandy dolomite, and sandy limestone. This sequence records the transition between continental red beds and shallow marine carbonates. The bed bearing the lingulids is composed of cross-bedded, light brown, clayey fine-grained sandstone. It is located at about 60 m below the top of the Bellerophon Formation (Prinoth, 2013; Figs. 2, 3a, b). The maximum flooding of the 4th sequence is referred to the late Changhsingian (Posenato, 2010).

2.2. The Lower Triassic lingulids

The Werfen Formation is a thick mixed terrigenous–carbonate succession which records the peak, survival and early recovery phases of the LPE (e.g., Broglio Loriga et al., 1983; Posenato, 1988; Broglio Loriga et al., 1990; Twitchett and Wignall, 1996; Posenato, 2008a,b, 2009; Hofmann et al., 2011). The older Triassic lingulids studied here come from the Mazzin Member, a unit mostly composed of marlstone and marly-silty mudstone, with frequent fossil accumulations interpreted as tempestites, deposited within a transition to off-shore sedimentary

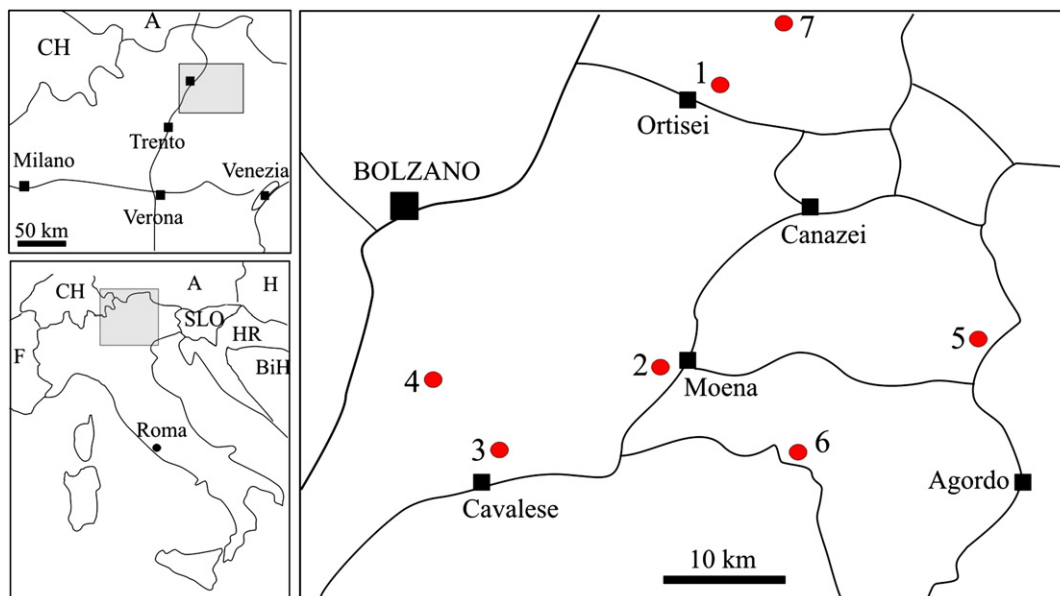


Fig. 1. Geographic location of the Dolomites outcrops where the studied lingulids were collected. 1, Monte Balest; 2, Malga Panna; 3, Cavalese; 4, Butterloch; 5, Avoscan; 6, Passo Rolle; 7, Passo Poma.

Download English Version:

<https://daneshyari.com/en/article/4466320>

Download Persian Version:

<https://daneshyari.com/article/4466320>

[Daneshyari.com](https://daneshyari.com)